

Im Dezember war dieses Verhalten bei keinem der Tiere mehr festzustellen und trat auch nicht mehr bis zur Beendigung des Winterschlafes auf. In Abbildung 2 ist jeweils für die Tiere I, II, V und VI der Grad der Temperatursenkung in % der Umgebungstemperatur für die ersten Winterschlafperioden bis zum Auftreten des erstmaligen Absinkens der Körpertemperatur auf den Wert der Umgebungstemperatur dargestellt. Deutlich gehen daraus auch die großen individuellen Unterschiede hinsichtlich dieses Verhaltens hervor.

Diskussion

Über eine unterschiedliche Dauer der Schlafperioden haben bisher PENGELLY und FISHER (1961) nach Untersuchungen an 7 Zieseln (*Citellus lateralis*) und STRUMWASSER et al. (1964) nach Beobachtung eines Tieres der gleichen Art berichtet. Sehr ausführliche Ergebnisse liegen von TWENTE und TWENTE (1967) vor. Diese Autoren haben ebenfalls an *Citellus lateralis* umfangreiche Untersuchungen über den Eintritt der ersten Winterschlafphasen sowie über die Relationen der Länge von Wach- und Schlafzeiten ausgeführt. Die ersten Winterschlafperioden traten bei diesen Tieren allerdings bei 5° C Umgebungstemperatur in der Zeit vom 24. 9. bis 15. 11. auf. Die ersten sechs Schlafperioden zeigten eine progressive Verlängerung ihrer Dauer, während gleichzeitig die Wachzeiten kürzer wurden. Die Autoren sprechen hier von einem „autumn pattern“. In der Zeit nach etwa sieben bis acht Schlafperioden konnten die Autoren eine Konstanz der Dauer aller Schlafperioden nachweisen, wobei die absolute Dauer der Schlafphasen sich als temperaturabhängig erwies. Die Autoren bezeichnen diese Zeitspanne als „winter pattern“. Gegen Ende der gesamten Winterschlafzeit zeigten die letzten 4 Schlafperioden wieder eine zunehmende Verkürzung, diese Phase wird als „spring pattern“ gekennzeichnet. Es ist eindeutig, daß die in dieser Arbeit für *Tamias (Eutamias) sibiricus* beschriebenen Phasen I und II diesen verschiedenen „sleep patterns“ völlig entsprechen.

Allerdings entsprechen sich die Ergebnisse nicht im Hinblick auf die Temperaturabhängigkeit der Dauer von Schlafphasen in Phase II. Es wäre denkbar, daß der Temperatureinfluß bei einem Temperaturunterschied von 5° C nicht meßbar ist. Ein Experimentieren bei tieferen Temperaturen als 15° C hielt ich aber nicht für günstig, da bei früheren Beobachtungen (JAEGER l. c.) bei Umgebungstemperaturen unter 10° C bei diesen Tieren keine Winterschlaflethargie zu beobachten war. Diese Frage bedarf aber noch einer genaueren Prüfung.

STRUMWASSER (1959) klassifizierte die Winterschläfer unter den Rodentia in drei Gruppen gemäß ihres sehr unterschiedlichen Verhaltens beim Eintritt des Winterschlafes: Eine erste Gruppe, zu der er den Goldhamster rechnet, zeichnet sich durch nach langer Vorbereitungszeit plötzlich auftretende, tiefe Lethargie aus. Eine zweite Gruppe, zu der Arten der Gattung *Perognathus* gehören, fällt nach kurzer Vorbereitung ebenfalls rasch in tiefe Lethargie, wogegen eine dritte Gruppe, darunter Ziesel und Murmeltiere, den Zustand tiefer und langer Lethargie erst allmählich erreichen. Zu dieser dritten Gruppe können wir auch den Burunduk rechnen.

STRUMWASSER hält äußere und innere Faktoren als Voraussetzung für das Eintreten von Winterschlaf für gleichbedeutend, ja in seiner schematischen Darstellung erachtet er die äußeren „permissive environmental factors“ als notwendige Bedingungen. In meinen Versuchen trat Winterschlaf aber bei Zimmertemperatur, Zwölfstundentag und beliebigem Futterangebot ein. Danach bestehen sicherlich Artunterschiede in den notwendigen, äußeren Konstellationen und ihrer Variationsbreite, bei der Winterschlaf noch eintritt. Beim Burunduk weichen diese äußerlichen Bedingungen offenbar nicht wesentlich von solchen ab, die bei voller Aktivität herrschen. Entscheidender ist bei ihm anscheinend eine innere Winterschlafbereitschaft.

Die anfänglichen kurz dauernden Lethargieperioden mit geringer Senkung der Körpertemperaturen werden von STURMWASSER (l. c.) als sog. „test drops“ bezeichnet. Diese „test drops“ sollten den Organismus des Winterschläfers über den „Stand der Winterschlafbereitschaft“ informieren und bei Erreichen eines ädaquaten Vorbereitungsstandes das Signal zur Einleitung der Tiefenlethargie geben. Schließt man sich dieser für die Tiere der dritten Gruppe recht einleuchtenden Hypothese an, so läßt sich hieraus sehr leicht eine Erklärung dafür ableiten, daß bei den Burunduks bei normalen und mittleren Umgebungstemperaturen die Lethargieperioden leichter eintreten als bei den tieferen Temperaturen. Höhere Umgebungstemperaturen stellen wesentlich geringere Anforderungen an die physiologisch-biochemischen Adaptionen, die zum Überleben längerer Lethargieperioden bei erniedrigter Körpertemperatur nötig sind. Die Vorbereitungen können kürzer sein. Die „test drops“ melden eher volle Bereitschaft, und wenn die inneren Faktoren übereinstimmen, kann die Lethargieperiode auf der entsprechenden Temperaturstufe beginnen. Die von mir selber (JAEGER l.c.) vertretene Ansicht, daß der Burunduk ein Kurzschläfer sei, ist wohl dahingehend zu erweitern, daß diese Tiere bei Temperaturen unter 10°C unter der Voraussetzung der Notwendigkeit einer langen und gründlichen Vorbereitung auf die Lethargie bei so tiefen Temperaturen erst gar nicht über das Stadium der „test drops“ hinauskommen.

Dies mag der Grund sein, warum Burunduks gerade bei winterlichem Wetter so oft im Freien zu sehen sind (vgl. LUTHER 1952), was zur Folge haben mußte, daß ihre Bereitschaft zum Winterschlaf nicht sehr hoch eingeschätzt wurde.

Zusammenfassung

Bei sieben männlichen Burunduks wurde die Dauer der Schlaf- und Wachphasen im Verlaufe einer Winterschlafperiode gemessen. Drei Tiere wurden bei 20°C , vier bei 15°C gehalten. Die Dauer der Schlafphasen war zu Beginn und am Ende einer Winterschlafperiode kürzer als in einer mittleren Zeitspanne, die mit dem Hochwinter zusammenfällt. Es wurden Eintritt und Gesamtdauer der Winterschlafperiode ermittelt; dabei zeigte sich, daß bei einem Temperaturunterschied von 5°C kein Einfluß auf diese Daten zu erreichen war. Bei vier Tieren konnte mit telemetrischer Methode die absolute Körpertemperatur während der Schlafphasen ermittelt werden. Es zeigte sich, daß bei den Tieren eine unterschiedliche Anzahl von Lethargieperioden die Winterschlafperiode einleiteten, bei denen die Körpertemperatur nicht auf die Umgebungstemperatur absinkt. Im Sinn von STRUMWASSER (1959) können diese frühen Lethargiephasen im Herbst als „test drops“ angesehen werden. Dadurch wird erklärbar, daß der Burunduk bei tiefen winterlichen Umgebungstemperaturen als Kurzschläfer gilt, nämlich dann, wenn „test drops“ dauernd eine ungenügende physiologische Winterschlafbereitschaft melden, die andererseits zum Überleben tiefer Körpertemperaturen notwendig wären.

Summary

*Duration of lethargic and active phases during the hibernating period of the asiatic chipmunk
Tamias (Eutamias) sibiricus Laxmann, 1796*

The duration of lethargic and active phases was measured in seven asiatic chipmunks (*Tamias [Eutamias] sibiricus*). Three animals were caged at 20°C other four were kept at 15°C . At the beginning and the end of the hibernating season the lethargic periods were significantly shorter than during a mid winter period. The temperature difference of 5°C had no significant influence on the date of entrance and duration of the hibernating period. In four animals where absolute body temperature could be measured by telemetric method it was shown that during a first variable couple of lethargic periods body temperature was not decreased down to environmental temperature values. This phenomenon was compared with the "test drop" theory of STRUMWASSER. In the case of the asiatic chipmunk the functioning of "test drops" could prevent the animal to fall into deep hibernation, when environmental temperature is very low, a fact which leads to the opinion that the asiatic chipmunk shows himself not a true hibernator, because he was frequently seen running around during winter-time.

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Variability in number and distribution of *Apodemus flavicollis* (Melch.) and *A. sylvaticus* (L.) in South Sweden

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1. Introduction

Apodemus sylvaticus (L.) is a very common small rodent in South Sweden which in most autumns occurs in large numbers in forest habitats (HANSSON 1967). The species also appears regularly on open fields (HANSSON 1968). *Apodemus flavicollis* (Melch.) is usually found in considerably smaller numbers and almost only appears in forest habitats, but may during certain years reach high numbers (cf. HANSSON 1967).

During a study of habitat selection and behaviour of the two *Apodemus* species at the Stenoffa Ecological Station in southernmost Sweden (cf. e. g. HOFFMEYER 1973), *A. flavicollis* was found in large and increasing numbers during 1972. An opportunity was thus presented to examine the population increase and the habitat distribution of *A. flavicollis* and the possible effects on the *A. sylvaticus* population. Long-term population studies in the area were used for the analyses and some particular examinations were also performed.

2. Methods

2.1. Small quadrat catches

The Stensoffa area was used as one of the sampling localities for a pan-Nordic monitoring programme concerning small rodents. Trapping was performed in four habitats with small quadrats (MYLLYMÄKI et al. 1971) during the autumn, late winter, spring and high summer. Population structure, reproduction and weight were determined for the animals caught.

2.2. Unsystematic live-trapping

Live-traps were put in the "best positions" in the forests and on grasslands in order to obtain as many animals as possible for the experiments. The trapping was non-regular but as there was a great trapping effort the catches are believed to be comparable in 1971 and 1972.

2.3. Long-term removal

Twenty live-traps were located in the garden of the Stensoffa Station since 1967. The station is situated in about the middle of a 10 ha abandoned field, mainly surrounded by forests but connected with other extensive abandoned fields. The shortest distance to a forest is about 75 m. The project and results will be treated in another context but it may be stated here that the catches partly reflect the population pressure for various species.

2.4. Examination of occurrence on fields in relation to distances to forests

2.4.1. Removal lines

Six lines of 14×2 live-traps were placed starting from inside beech forests and out onto sandy, abandoned fields for two days during September 1972. The distance between trap stations was 15 m with 3 stations in the forest, 1 station on the forest edge and 10 stations thus extending 150 m out onto the fields.

2.4.2. Random quadrats

Ten small quadrats with live-traps were randomly distributed on sandy, abandoned fields during August and October 1972 so that the distance to the nearest forest was variable. Animals were trapped for four days and removed each day.

3. Habitats

3.1. Beech forests

This habitat consisted mainly of pure mature beech, *Fagus sylvatica*, but some mature oaks, *Quercus robur*, and pines, *Pinus silvestris*, were also present. The field layer was rather poor and contained low herbs and *Rubus idaeus*.

3.2. Reforestations

These areas had been reforested with spruce, *Picea abies*, after the beech forest had been cut. A luxuriant field layer dominated by *Chamaenerion angustifolium* and *R. idaeus* was also present.

3.3. Abandoned fields on mineral soil

These habitats were sandy, dry areas with a rather open grass cover dominated by *Dactylis glomerata*.

3.4. Abandoned fields on peat soil

This habitat type consisted of wet areas with a luxuriant vegetation cover of mainly grasses and sedges, e. g. *Deschampsia caespitosa* and *Carex nigra*.

4. Results

4.1. Small quadrat catches in four habitats during 1971—73

In all four habitats examined, there was a change in the proportions of *A. flavicollis* and *A. sylvaticus* trapped during 1971—73 (Fig. 1). The number of *A. sylvaticus* decreased rapidly from autumn, 1971 to late winter and spring, 1972. There

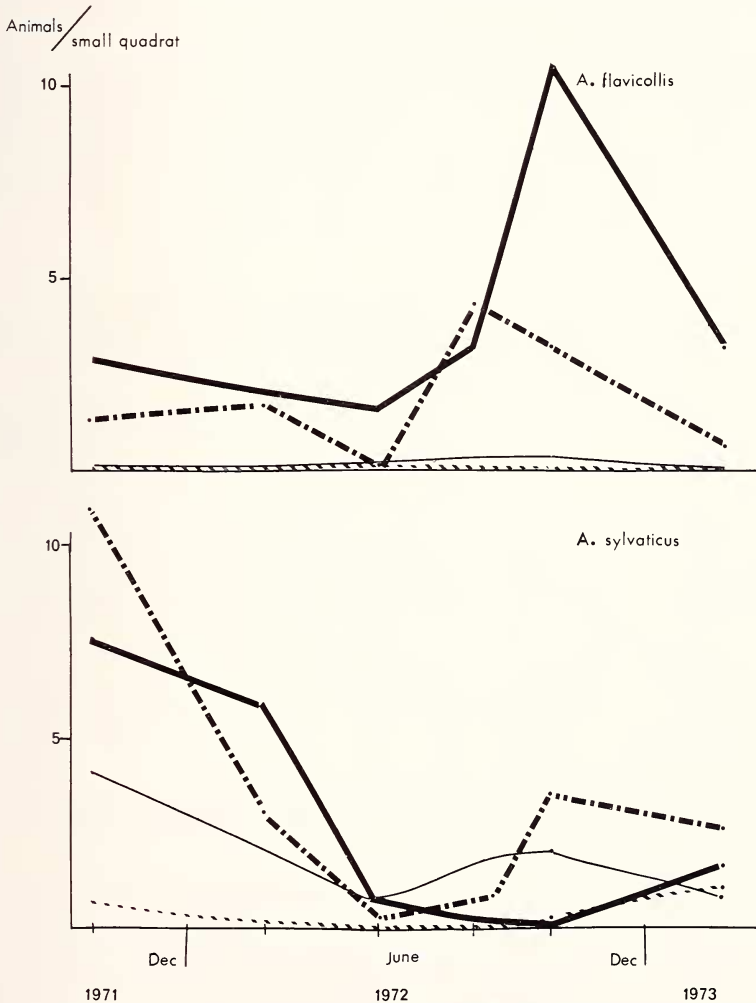


Fig. 1. Mean number of animals caught per small quadrat in four habitats during 1971—73. About ten small quadrats were randomly distributed in each habitat during each trapping period ——— = beech forest; -.-.- = reforestation; ——— = sandy, abandoned fields; - - - - = abandoned fields on peat soil

was only a slight increase in "field" habitats (with generally more captures on sandy than on peat soil) during the summer-autumn period of 1972 and a further decrease for the beech forest. For *A. flavicollis*, there was a slight decrease until the spring of 1972 and thereafter a rapid increase, especially for the beech forest. For both species, highest numbers were obtained during the autumns of 1971 and 1972 in the same habitats, i. e. in the beech forest for *A. flavicollis* and in the reforestations for *A. sylvaticus*. However, during 1972 as compared with 1971, there were significantly more *A. flavicollis* caught per quadrat in the beech forests ($t = 3.24$, $p < 0.01$) and fewer *A. sylvaticus* in the beech forests ($t = 4.73$, $p < 0.001$) and the reforestations ($t = 5.58$, $p < 0.001$). During the late winter of 1973, there was a pronounced decrease in the *A. flavicollis* population. The *A. sylvaticus* population was now more evenly distributed in the four habitats and there was an increase in the numbers present in the beech forest.

The inverse relations for catches of *A. flavicollis* and *A. sylvaticus* could have been due to e. g. competition for traps or differences in the selection of micro-habitats. Both these conditions ought to have resulted in negative correlations between catches of the two species in the quadrats. Examination showed insignificant correlations for the beech forest ($r = -0.54$) and the reforestations ($r = +0.04$) for the autumn of 1971, but a significant positive correlation for the reforestations for the autumn of 1972 ($r = +0.64$, $P < 0.05$). These were the only habitats and times with considerable numbers of animals of both species.

Table 1

Population structure and weights of *A. flavicollis* and *A. sylvaticus* caught in small quadrats in various habitats during the autumns of 1971 and 1972

Habitat	Year	Juv.	Ad.	Subad.	Post repr.	Σ specimens	Weight of subadults ($\bar{x} \pm SE$)
<i>A. A. flavicollis</i>							
Beech forest	1971	2	12	11	6	31	30.0 \pm 1.4
Beech forest	1972	1	37	33	24	95	27.9 \pm 0.8
Reforestations	1971	0	3	4	3	10	26.9 \pm 1.2
Reforestations	1972	0	8	15	7	30	31.1 \pm 1.3
<i>B. A. sylvaticus</i>							
Reforestations	1971	4	2	62	8	76	17.5 \pm 0.3
Reforestations	1972	3	4	17	10	34	16.2 \pm 0.3
Abandoned fields	1971	4	11	20	12	47	16.2 \pm 0.5
Abandoned fields	1972	8	3	28	8	47	16.0 \pm 0.4

The population structures during the two autumns were examined for the beech forests and the reforestations for *A. flavicollis* and in the reforestations and on abandoned fields for *A. sylvaticus* (Tab. 1). As only one *A. sylvaticus* was caught in the beech forest during the autumn of 1972, a comparison was impossible for this habitat. The population structures of *A. flavicollis* were very similar for the two years while there was a considerably lower proportion of *A. sylvaticus* subadults in the reforestations during 1972. (When compared to the rest of the catches, $\chi^2 = 11.57$, $P < 0.001$). The weights of these subadults were also significantly lower in 1972 than in 1971 ($t = 3.24$, $P < 0.01$). On abandoned fields with very few *A.*

flavicollis, there were no such changes. Sub-adults of *A. flavicollis* in the reforestations weighed more during 1972 than as compared to 1971 ($t = 2.34, P < 0.05$).

4.2. Live-trapping during the autumns 1971 and 1972

The unsystematic live-trapping (Tab. 2) revealed the same pattern of distribution for the two species, i. e. *A. sylvaticus* was most common in both the beech forests and on the abandoned fields during the autumn of 1971, and *A. flavicollis* appeared in large numbers in the forests during 1972, while *A. sylvaticus* was almost only found in the fields. Live-trapping (multiple-catching traps) yielded a relatively larger number of *A. flavicollis* in the forests during 1972 than of *A. sylvaticus* in 1971.

4.3. Long-term removal

The number of continuous removal catches (Fig. 2) differed for the two years mainly in the great number of *A. flavicollis* caught from June until November–December, 1972. In 1971, there were only rather occasional catches of *A. flavicollis* for the same period. For both years there were a great number of *A. sylvaticus* caught. In 1972 the summer-autumn increase was delayed, i. e. the first animals were not caught until the middle of August, whereas the increase in 1971 started during June. A comparison of the distribution of catches of *A. sylvaticus* for the two years showed a significant difference ($\chi^2 = 37.62, P < 0.001$). However, in both years the peak fell in September, which was also the case for *A. flavicollis* in 1972.

4.4. Distributions on fields of the two species during the autumn of 1972

The lines of traps extending from forests and onto the fields (Fig. 3) showed that this year the forest edge was a clear limit for the penetration of the grassland-living *A. sylvaticus*. Specimens were caught in trap stations at each unit distance outside the forest but in none inside the forest. *A. flavicollis* was caught in great numbers inside the forests but a few were also caught on the fields. The numbers caught at

Table 2
Catches from unsystematically placed live-traps during August—October 1971 and 1972

	Beech forest				Abandoned fields			
	1971	1972	1971	1972	1971	1972	1971	1972
<i>A. flavicollis</i>	99	217	20	35	0.07	0.21	0.01	0.02
<i>A. sylvaticus</i>	140	7	212	188	0.10	0.01	0.14	0.09
	1428	1032	1470	2172				
	\sum trap nights	\sum trap nights	\sum trap nights	\sum trap nights	\bar{x} animals trap	\bar{x} animals trap	\bar{x} animals trap	\bar{x} animals trap
	\sum animals	\sum animals	\sum animals	\sum animals				

the two ends of the lines were due to an edge effect appearing when the distance between trap stations is smaller than the home ranges of the species.

When the correlations were examined between catches in quadrats on the fields and the distances to the forests (Tab. 3), significant negative correlations were found for *A. flavicollis* and for *A. sylvaticus* during August. No *A. flavicollis* were captured in the fields during October. The correlation to the distance to the beech mast/acorn forests was not better than the correlation to only the nearest forest edge. Obviously *A. flavicollis* only penetrated the fields in the near vicinity of the forests. There was a tendency of *A. sylvaticus* to gather close to the forests.

5. Discussion

In 1972, the numbers of *A. flavicollis* increased very greatly but there was no noticeable change in the habitat distribution from 1971. The increase only occurred

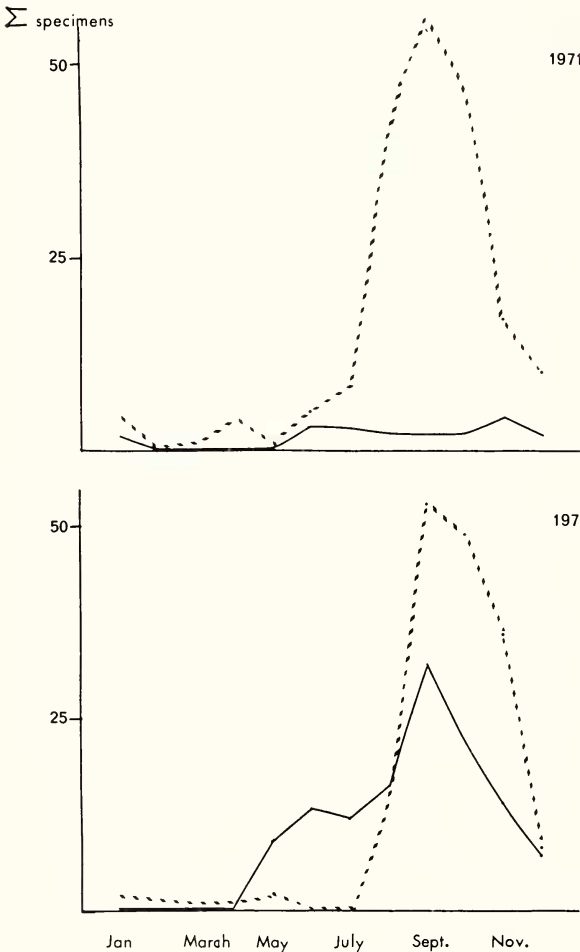


Fig. 2. Animals caught by continuous removal trapping at the Stensoffa Ecological Station. — = *A. flavicollis*; - - - = *A. sylvaticus*

in the beech forests and in the forest-like reforestations. On the other hand, the change in habitat distribution of *A. sylvaticus* from 1971 to 1972 was very distinct. There was a marked decrease in the forest populations in 1972. However, this species seemed to prefer forest-like habitats, as even in this year the largest numbers were caught in the reforestations. The number of *A. sylvaticus* caught on abandoned fields was almost unchanged at the time of the decrease in the forests.

The population structure and physiology of *A. sylvaticus* were affected in habitats where *A. flavicollis* occurred, i. e. in the reforestations. There seems to have been a low recruitment in high and late summer, 1972 as few subadults were caught later on. However, reproduction and spring survival appeared to be normal with the usual number of post-reproductive animals present during the autumn 1972. The low summer recruitment might be the reason for the delayed immigration to the Stensoffa garden traps.

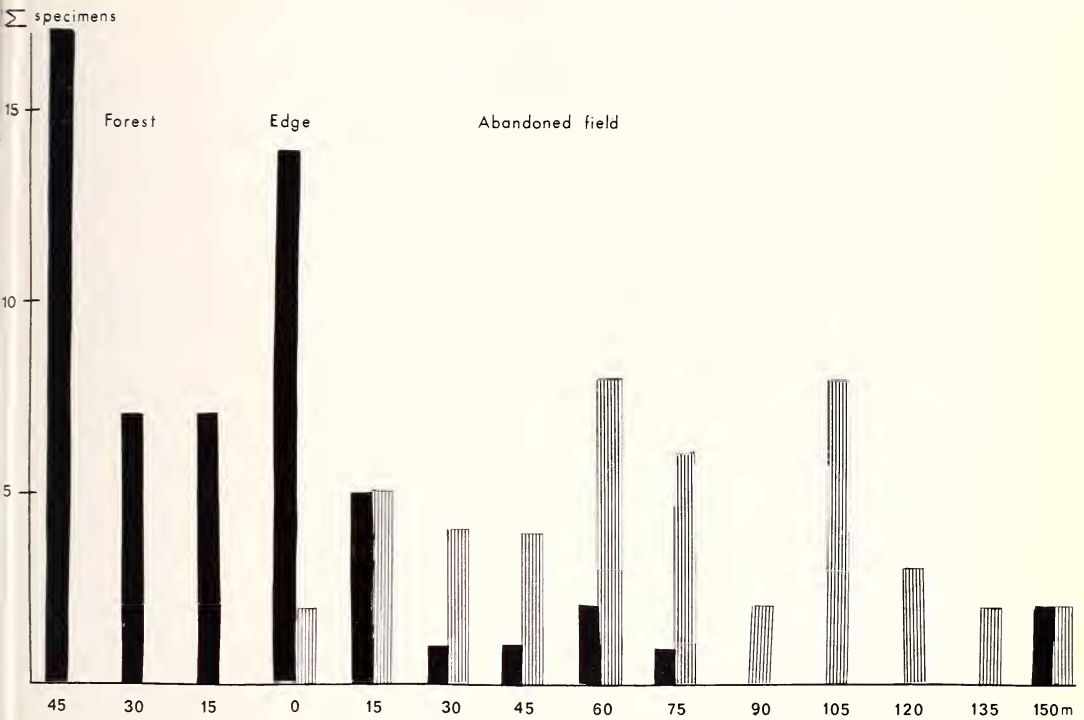


Fig. 3. Distribution of catches in six removal lines extending from beech forest out onto sandy, abandoned fields. ■ = *A. flavicollis* ▨ = *A. sylvaticus*

There are thus clear indications that *A. sylvaticus* was negatively affected by *A. flavicollis* during the peak occurrence of the latter. HOFFMEYER (1973) experimentally found that *A. flavicollis* were able to dominate *A. sylvaticus* in a passive way. Such a dominance, perhaps enhanced by aggressiveness (it has been demonstrated that breeding animals are more aggressive than nonbreeding, SADLEIR 1965, WATSON, MOSS 1970) — may explain the decrease of *A. sylvaticus* in the forests and the limitation of this species to the fields during the summer of 1972. Early summer may be a critical period for *A. sylvaticus* with regard to food conditions (HANSSON 1971). *A. flavicollis* in general eats the same kinds of food, and a domi-

Table 3

Correlation between small quadrat captures on abandoned fields and the distances to forest habitats

NS = non-significant

Distance	A. sylvaticus				A. flavicollis	
	August		October		August	
	r	P	r	P	r	P
Forests generally	-0.64	<0.05	-0.47	NS	-0.72	<0.05
Beech-oak forests	-0.62	NS	-0.52	NS	-0.64	<0.05